

# PLANT PHYSIOLOGY AS SACHS FOUND IT<sup>1</sup>

ERNEST S. REYNOLDS

*Physiologist to the Missouri Botanical Garden*

*Associate Professor in the Henry Shaw School of Botany of Washington University*

## FORMATIVE INFLUENCES

Julius von Sachs, in whose honor this celebration is held, began his work at a strategic time in the development of plant physiology. The foundational sciences of chemistry and physics had emerged from the restraints imposed upon them by the spirit of the Middle Ages and the bases for many of the modern concepts had been laid. Since the development of modern plant physiology was necessarily dependent upon a scientific understanding of the laws of physics and chemistry the best that could be expected of primitive biological studies was an accurate description of the apparent reactions of organisms. Although the ancients, including the most noted of the philosophers, had a modicum of essentially correct concepts of animal physiology, because of the subjective element in human physiology they failed, due to the objective character of plants, in understanding even as much concerning them as they knew of animals. The nutritional dependence of plants upon their environment, together with a realization that some method of transfer of materials in the plant is necessary, the obvious importance of seeds in the continuity of life and certain empirical observations upon apparent values of certain fertilizing materials—these constituted essentially the stock in trade of the ancients. Later, analogies between the better-known activities of animals, especially of the human body, and the supposed reactions of plants resulted in the accumulation of certain hypotheses which, although unsupported by experiments or adequate observation, have in some instances more recently been demonstrated as correct. These, however, were scarcely more than lucky guesses. It is true, nevertheless, that progress in animal physiology has often been of great value in suggesting profitable lines of investigation

<sup>1</sup> A paper read at the celebration held at the Missouri Botanical Garden, December 27, 1931, in honor of the one-hundredth anniversary of the birth of Julius Sachs.



in the physiology of plants. During the history of our science there has been an interesting oscillating from the extreme of the complete dependence upon analogies with animal physiology, of the ancients, to the opposite extreme, as exemplified by Schleiden (1849), who refers to "the fanciful analogy between the physiology of animals and of plants." "In consequence," he continues, "of the use of this absurd analogy, almost all of the works which have hitherto appeared on vegetable physiology are perfectly worthless, for in no instance have they adopted the only true fundamental position, namely, the essential peculiarity of vegetable life." The pendulum was to swing back, due in no small measure to Schleiden's further studies, to a recognition of the essential unity of life, together with a proper regard for its numerous modifications and diversities. Not only did advances in animal physiology aid in establishing a point of view in the study of plants, but two other influences also were of prime importance in giving a proper impetus to the formation of a true science of vegetable physiology.

Developments in general microscopy soon brought more sharply into view the problems of plant structure. Malpighi and Grew, beginning in 1671, illustrated and carefully described much of the tissue structure of plants, although it seems clear that they did not conceive of these organisms as built up of the unit structures now known as "cells"; nor was it until von Mohl, about 1830, a hundred and fifty years later, clearly expounded the proposition that the cell is the unit of structure, that there was a general acceptance of this doctrine. Nevertheless, the exact knowledge of the general anatomy of the stem led to numerous queries as to the utility of the various units to plants. Thus a fairly correct understanding of anatomy stimulated a study of physiology. Malpighi had concluded that the leaves of plants are important in their nutrition, and before that von Helmont's famous experiment with the willow tree had demonstrated the fallacy of the ancient belief that elaborated food from the soil is the chief source of plant substance. Yet as late as the publication of Schleiden's and von Mohl's texts, it was found necessary to controvert vigorously this belief in the absorption of large quantities of organic food from the soil.



Stephen Hales in 1727 published his 'Vegetable Staticks,' and as this was the first considerable attempt to study plant physiological problems by exact measurements it is especially important in examining the bases of the modern science. Among the phenomena studied were transpiration, the pulling action of leaves on the transpiration stream, the reduced pressure in the plant during active transpiration, stump pressures, pressures developed in spring vegetation, the alleged circulation of sap, presence of air in stems, the free passage of water in either direction through the stem when leaves are actively transpiring, and the rate of passage of water upward due to leaf pull contrasted with the downward movement under the weight and pressure of several feet of water. In many of these problems he came to essentially correct conclusions and remained for a hundred years the brightest light in the field of the application of physics to vegetable physiology.

Robert Brown, about 1833, is credited with having discovered and named the cell nucleus, the movement of protoplasm, and most important, from the theoretical physiological aspect, the dancing movement of small particles suspended in liquid which was named for him the Brownian movement.

It is to the rapid development of chemistry, however, that we must look for the main stimulus which finally established plant physiology upon a modern scientific basis. Just before the elimination of the phlogiston theory in chemistry, Priestley (1790), in the course of his studies upon atmospheric gases, published a series of studies upon the relations of plants to the air. Some of the section titles of his work, giving an indication of his contributions to the subject, are as follows:

"Of the Restoration of Air, in which a Candle has burned out by Vegetation."

"Of the Restoration of Air infected with animal Respiration or Putrefaction, by vegetation."

"Of the Growth of Plants in dephlogisticated Air."

"Of the State of Air confined in the bladders of Sea Weed."

"Of the spontaneous Emission of dephlogisticated Air from Water containing a vegetable green Matter."

"Of the Purification of Air by Plants, and the Influence of Light on that Process."



Sachs (1906), in his 'History of Botany,' says: "The establishment of the fact, that parts of plants give off oxygen under certain circumstances, did little or nothing to further the theory of nutrition; and that was all that vegetable physiology owes to Priestley." It seems to the writer, however, that, in view of the above quoted section titles, this dismissal of Priestley with such faint praise is hardly justifiable if one reads carefully his publications. He established the facts that light is essential to the process of giving off oxygen and that in the dark there is definite injury to air, viewed from the point of view of the phlogiston theory. Sachs is further in error when he says later: "Priestley himself did not suspect that the deposit in question, afterwards known as Priestley's matter and found to consist of Algae, was a vegetable substance."<sup>1</sup> He not only "suspected" that it was a "vegetable substance" when he first saw and experimented with it, but in his Section VII definitely states that other scientists better versed in botany had examined it for him and had determined it as a plant; and he finally says he is convinced that it is a plant which reached the jars through its "seeds" either having been in the water to begin with or, floating in the air, had entered due to loose stoppers. He criticized Ingen-Housz even for hypothesizing a spontaneous generation of the plant, rather than accepting the origin through outside infection.

Ingen-Housz (1779), however, published a much more extended study of the whole problem in his 'Experiments upon Vegetables' in which he demonstrated the use of carbon dioxide as the source of carbon for plant nutrition, and the relation of light and the green color of plants to the process. He also stated clearly that atmospheric oxygen is necessary for continued life in plants. Senebier (1800), and especially de Saussure (1804), added much to the preciseness of the chemical demonstrations of the relationship of plant nutrition to carbon dioxide and water and of respiration to the atmospheric gases. Studies of the mineral content of plants and of the source of the nitrogen used by plants completed a reasonable chemical foundation on which new advances could be built. However, much of this new material was either not accepted or at any rate had not become generally

<sup>1</sup> Sachs seems not to have referred to Priestley's publication of 1790.



diffused among botanists until the beginning of Sachs's investigations.

### THE STATUS OF PLANT PHYSIOLOGY IN 1850

With this brief review of the main sources of stimulation for the establishment of a science of plant physiology we may now turn more particularly to the status of the subject when Sachs appeared in the field. It is convenient to select the year 1850 as approximately the end of the pre-Sachs period, especially because at about this time von Mohl (1852) published his 'Principles of the Anatomy and Physiology of the Vegetable Cell,' which indicates especially well the status of the subject at that period. A short time before this Schleiden's (1843) 'Grundzüge der Wissenschaftlichen Botanik' had appeared, and this also presents a picture somewhat different from von Mohl's summary. The term "protoplasm" had just been accepted, but there was no clear understanding of the usual process of cell formation, as is indicated in this statement by Schleiden (1849): "The process of the reproduction of cells by the formation of new cells in their interior is a general law in the vegetable kingdom and is the foundation of the production of cell-tissue." Nevertheless, the importance of a clear understanding of the process was clearly recognized in his further statement that "The question respecting the multiplication of the cells consequently includes the origin and the life of the whole plant, which remains altogether obscure to us previous to the elucidation of this relation."

The group of catalysts had been recognized and named by chemists; and the general catalytic action of the "slime" or "protoplasm" had been discovered. These observations led finally to the recognition of specific catalytic action in plants. Thus Payen and Persoz in 1833 had named diastase and had cleared up some of the earlier misunderstandings concerning the changing of starch to sugar; and Liebig and Wöhler had recognized and named emulsin in 1837 as a substance acting upon amygdalin. Still the significance of these enzymes as representatives of a class of substances was not appreciated, and the conditions governing their activities were not well understood. Nevertheless, a few foundation stones for a study of enzyme chemistry had been laid.



Following the early observations by Nollet and others, Dutrochet, about 1830, developed the concept of endosmosis as an explanation of absorption by the plant, and thereafter a general extension of the theory of endosmosis offered an explanation of the passage of water from cell to cell throughout the parenchyma tissues. However, no careful quantitative determinations of pressures were made and the theories were vague. Thus von Mohl (1852) says: "Since the discovery of endosmose, most vegetable physiologists have assumed it as an axiom that the absorption by cells depends wholly and solely upon the laws of endosmose, none of the peculiar forces of the living cell co-operating. All the conditions to bring about strong endosmosis do really exist in the living vegetable cell, namely, a membrane freely penetrable by watery fluids; on the one side of this the cell-sap which contains proteine substances, dextrine, sugar, etc., in solution, on the other side the water occurring in nature, in the state of an extremely diluted saline solution. This renders it readily explicable how cells which are laid in water swell up rapidly, in many cases, if they contain a concentrated protoplasm and have not firm walls (e.g., many pollen-grains), the powerful absorption of water causing them to burst; and how, on the other hand, if they are laid in a strong solution of sugar, gum, etc., they become emptied and collapse. Under these circumstances, the assumption that the absorption of the cells will be regulated by the laws of endosmose, is fully justified, yet special proofs of this can only be partially advanced, because on one side the phenomena of absorption are too little known in many respects, and on the other side the theory of endosmose is not yet perfect enough to allow of our making out in all cases the share it has in any given phenomenon." The limitations of the term "endosmosis" were not clear and even yet there is a lack of clarity in the usage of terms and the concepts included. For example, osmosis is sometimes still made to include the passage of both solute and solvent through the membrane, which at that time was believed to be the cell wall, although there are obvious advantages in restricting the term to the diffusion of the solvent and thus recognizing the process as a special case of diffusion in which pressures are developed and maintained. The diffusion of



solutes then falls into its place as an example of the general process.

The universal solvent action of water for all substances, including gases, entering the plant was well recognized. Quantitative determinations of the mineral content of plants had been made, which indicated the relatively small quantities necessary and the range of salts usually present. These data had also indicated a problem less easily explained, however, namely, why several kinds of plants living upon the same soil may accumulate different proportions of the various soil solutes. Liebig's hypothesis of excretion was offered by him to account for this phenomenon by assuming no differential permeability but a subsequent excretion of supposedly toxic mineral substances. Later, the experiments of others indicated differential absorption.

The problem of transportation in the plant was in an active state of discussion. The older vegetable anatomists, Malpighi and Grew, had studied the vascular system and described the elongated tubes as "tracheae" which, so far as they could detect, always contained air. Others, through unconvincing experiments, had stated that these tubes were the water-conducting channels. Schleiden (1849), in various portions of his 'Principles,' called attention to the incomplete nature of the evidence, and his conclusions are clearly indicated thus, "That the vessels convey only air, and no juices, may be seen by any one possessing the least physical knowledge, on the most cursory glance at a longitudinal section of a plant"; and again, "The so-called vessels in most plants never convey sap; and with others it is probable that they convey it only during a few weeks while the new buds are forming." He inclined toward the belief that all transfer of fluid in plants was from cell to cell by some osmotic process, but admitted a possibility that at certain seasons of the year in some plants, or under pathologic conditions, sap might pass into and possibly through the fully formed tracheae.

An example of the necessity of a clear differentiation between the solute and the solvent in discussing the subject of sap transfer is seen in the following statement from von Mohl (1852): "All these explanations of the movement of the sap bear reference only



to its ascent, not one of them applies at all to the descent of the elaborated sap. If the bark and the cambium layer attract the nutrient matter from the leaves because their cells contain a more concentrated sap than the cells of the leaves, it is not evident why they cannot draw the sap directly from the root and the wood, instead of by the long circuit through the leaves, and why the bark is wholly incapable of carrying sap upwards." It must be remembered that von Mohl in 1852 was inclined to believe that the passage of water upward must be in the parenchyma cells of the wood by the power of endosmosis induced by transpiration from the foliage, and that there is a corresponding downstream in the bark. In the above quotation, then, there would have been no special problem had he clearly discerned that, on the basis of diffusion, the passage of solutes from cell to cell must be from regions of greater to those of lesser concentrations and that they must move independently of the direction of the solvent.

Transpiration is one of the activities of plants which was recognized by early observers and studied somewhat thoroughly by Hales. The rates and total amounts of water loss were determined for a fair range of representative plants and environments so that the essential unity of transpiration and physical evaporation had been accepted. Schleiden believed that transpiration by concentrating the sap in the leaf cells caused a progressive concentration of sap downward and thus furnished, together with the osmotic action of cells, an adequate explanation of the passage of liquids upward. Guttation was known in some cases and the specialized structures through which it takes place had been studied carefully.

The more common of the mineral elements which are considered as essential to plant growth had been studied; and considerable knowledge of specific chemical compounds from plants had accumulated. The uniformity of certain types of compounds, especially of sugar-like nature, had suggested some nutritional importance for them. The four classes of compounds, carbohydrates, not yet so named, organic acids, oils, and proteins had been distinguished.

As already indicated, the essential outline of photosynthesis



had been drawn but not all of the demonstrations had been fully accepted, and the term respiration still frequently included all gaseous exchanges by plants although von Mohl pointed out the desirability of using it in the restricted sense used in animal physiology.

Ammonia and its salts supplied through the roots appeared to be the main if not sole source of nitrogen, while the free nitrogen of the atmosphere had been ruled out of consideration by the work of several investigators. Although it was considerably later that the nitrifying power of soil organisms was offered as an explanation of the renewal of nitrogen in the soil, and it was believed that the continuous supply of nitrogen for plants was through the ammonia of the atmosphere, still some believed in a slow automatic ammonification in the soil.

The curious milk-sap theory of Schultz (1823-41) is an example of the extremes to which a theorist may go. He supposed that milk-sap was the exact analogue of the blood of animals and claimed that circulation, coagulation, and blood corpuscles were all duplicated in the phenomena which he observed in the milk tubes. This concept was sufficiently important for von Mohl to devote considerable time and argument to demonstrate its fallacies. Schleiden, in a characteristic passage, thus disposes of the older work: "On the subject of these structures, and especially the milk-vessels, I am rather afraid of saying too much than too little, for owing to the total neglect of a correct, scientific method and the purile sporting with hypotheses, without any foundation or guiding principle, the question respecting them is loaded with such a heap of nonsense that the best way in beginning upon it is, in the first place, to throw overboard all that has hitherto been done and commence entirely *de novo*, instead of undertaking the thankless task of cleansing this true Augean stable." The obvious nutritional difference between fungi and green plants had been studied experimentally to some extent from the time when it was demonstrated that the fungi did not absorb carbon dioxide in the light.

An interesting concept of Schleiden concerns the place in which elaboration of the nutritional substances occurs. He believed that the water and its inorganic salts and other necessary sub-



stances become elaborated in each cell so that, as he remarked, "nothing remains for the leaves to assimilate." Thus it was not necessary to have a means of transfer of food substances from the leaves to other parts of the plant and he denied any downward flow of sap in the bark. He appears to have believed that the carbon dioxide absorbed by leaves is conducted through the internal atmosphere to all parts of plants. Thus he says, "The conclusion that the carbonic acid found in the leaves is consumed by them is about as rational as the inference would be, from the respiratory movements of the nose and mouth, that the brain performed the functions of the lungs."

Schleiden lists as one of the main problems of seed germination: "An accurate determination of the degree of heat present during germination and a comparison of the same with the quantities of carbon and hydrogen which are consumed." Von Mohl clearly indicated the rapid loss of sensitivity and subsequent early death of plants cut off from an oxygen supply, thus calling attention to the close analogy between animal respiration and that of plants. The heat produced by plants was directly associated with the respirational process. The modern interpretations of gaseous exchanges between the plant and the atmosphere were not fully accepted at this time although it was known that carbon dioxide provides the carbon supply for green plants. Schleiden, however, stated in 1849 that, "It would appear that the exhalation of oxygen and the absorption of carbonic acid gas never stand in immediate relation with each other," and he saw in the exhalation of carbon dioxide only the beginning of decay. On the other hand, von Mohl, in his 'Anatomy and Physiology of the Vegetable Cell' published in 1852 clearly distinguished between the nutritive and the respirational processes involving the atmospheric gases.

A "fermentation-fungus" had been discovered and it had been suggested as the cause of the process of fermentation, but there was still no clear recognition of the essential nature of the yeast organism and its relation to the fermentation process.

The three main phases of the growth process, cell formation, cell enlargement, and cell differentiation, had been distinguished, but the details of these processes had yet to be filled in.



Due to the almost slavish adherence to the doctrine that all processes in animals must find their exact equivalent in plants, efforts were constantly made to demonstrate a method of excretion which would rid plants of injurious substances. Liebig believed that this was accomplished through the roots, at least to a considerable degree. Others, as, for example, von Mohl, pointed out that no experimental data had been adduced to provide for any but insignificant quantities of substances. A doctrine at that time which was used to uphold the excretion hypothesis taught that there must be an exosmosis to balance the endosmosis, and this then in the roots resulted in excretion of injurious materials. There had arisen at this time also a suggestion that toxic root excretions or the decayed remains of plants poison the soil for the plants producing them. While no experimental data were available the observations on crops had made this soil toxin hypothesis seem probable.

Schleiden's theory of the organization of the embryo from the tip of the pollen tube had just been displaced by the careful studies of Amici and Hoffmeister demonstrating the presence of the egg-cell in the embryo sac and the fertilizing action of the pollen tube. Sperms had been seen in the Cryptogams, and the essential features of the fertilizing process had been well described by several investigators.

Geotropism was on the verge of being discovered, for Knight's work had already been published, demonstrating reaction to centrifugal force, yet as late as Schleiden's 'Principles' it is stated that, "We know nothing at all respecting the cause of the direction taken by the germinating plant" and the action of gravitation as a stimulus was not accepted. The directional action of light on the stem was recognized, and the "sleep" reaction of many leaves was a well-known phenomenon. However, Sir Humphrey Davy, in his 'Elements of Agricultural Chemistry,' as late as 1813, had denied the concept of irritability in plants.

Controversies at this period were numerous, due to preconceived notions, inaccurate observations, and misinterpretations. While in the main Schleiden was a progressive scientist, there were several problems in which, because he took the cautious,



conservative attitude, he failed to espouse the new and correct ideas. While his criticisms of his predecessors are often severe and he often places little reliance on their work, this attitude seems to be due largely to his keen appreciation of the necessity of controlled experiments and of accurate and frequently repeated observations. One other source of his strictures was his repudiation of the popular method of almost complete dependence upon analogies between plants and animals. Although his extreme attitude was finally to be overthrown yet no doubt he was correct in believing at that time that these analogies were too easily accepted without adequate scientific evidence.

It is clear then that at the beginning of Sachs's activity the general outlines of our new plant physiology had been developed, but many of the major concepts were still seriously questioned while many important details and some major fields needed careful experimental study. Moreover, the separation of this field of investigation from that of general botanical studies had not taken place.

### BIBLIOGRAPHY

- Hales, Stephen (1727). *Vegetable staticks: or, an account of some statical experiments on the sap in vegetables: being an essay towards a natural history of vegetation. Also, a specimen of an attempt to analyse the air, . . .* London, 1727.
- Ingen-Housz, J. (1779). *Experiments upon vegetables, discovering their great power of purifying the common air in the sun-shine, and of injuring it in the shade and at night.* London, 1779.
- Priestley, Joseph (1790). *Experiments and observations on different kinds of air, and other branches of natural philosophy, connected with the subject.* Vol. 3, Book IX, Part I. Birmingham, 1790.
- Senebier, J. (1800). *Physiologie végétale contenant une description des organes des plantes, & une exposition des phénomènes produits par leur organisation.* 1-5. Genève, 1800.
- de Saussure, T. (1804). *Recherches chimiques sur la végétation.* Paris, 1804.
- Schleiden, J. M. (1843). *Grundzüge der wissenschaftlichen Botanik.* 1842-1843.
- Schleiden, J. M. (1849). *Principles of scientific botany; or, botany as an inductive science.* Trans. Edwin Lankester. London, 1849.
- von Mohl, Hugo (1852). *Principles of the anatomy and physiology of the vegetable cell.* Trans. Arthur Henfrey. London, 1852.
- von Sachs, Julius (1906). *History of botany (1530-1860).* Trans. Henry E. F. Garnsey. Rev. Isaac B. Balfour. Oxford, 1906.